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GEOMETRIC MORPHOMETRIC ANALYSIS OF *PAN* FRONTAL BONE
MORPHOLOGY

by

Allen Myhra

A THESIS

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GEOMETRIC MORPHOMETRIC ANALYSIS OF *PAN* FRONTAL BONE MORPHOLOGY

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University of Nebraska, 2015

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This study employs geometric morphometric methods to investigate the morphology and shape change of the frontal bone for *Pan troglodytes* and *Pan paniscus*. Unlike previous work on the topic, this research analyzed morphology and ontogenetic shape change in a single bone of the cranium, namely the frontal bone. Frontal bone shape was compared between juvenile *Pan troglodytes* and *Pan paniscus* and the ontogeny of the bone was assessed in *Pan paniscus* infants and juveniles. Analyses were performed on frontal bone morphology with and without the browridge in order to assess the morphology of the frontal apart from influences affecting the browridge. Results of ANCOVA with principal component shape variables indicate that the frontal bone shape differs between species ($P=.000$) and between infant and juvenile *Pan paniscus* for log centroid size ($P=.109$), but this shape change occurs largely in the browridge. Results for the frontal without the browridge do not significantly differ in shape between species for PC1 ($P=.205$) and PC3 ($P=.113$) and between *Pan paniscus* life stages for PC3 ($P=.103$). These results have implications for current and future work as they contribute to a growing body of knowledge aimed at understanding the complexities of cranial growth.

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CHAPTER 1: INTRODUCTION

The study of the genus *Pan*, our closest living relatives, has allowed biological anthropologists to make informed hypotheses about the evolution of humankind and what factors were responsible for such dramatic changes. In recent years, comparative studies of chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) have become more common due to the varied phenotypic differences witnessed between the two closely related species. Considering that the species diverged evolutionarily approximately 1 to 2 million years ago (Horai et al. 1995; Hey 2010), the differences in behavior, morphology, and even cognition are astounding. These differences can inform researchers about the potential pathways in which evolution has occurred for hominin species.

One such focus concerns the ontogenetic trajectories of the two *Pan* species. The study of growth and development is essential for understanding the evolution of a species, as changes in growth and development are considered to be responsible for derived features in descendent species. Heterochrony, a change in developmental timing, is argued to be the cause of the differences observed between the two *Pan* species (Shea 1983). Specifically, *Pan paniscus* appear to be paedomorphic, or have juvenilized *Pan troglodytes* characteristics. Since Shea's (1983) publication, researchers have attempted to find concrete evidence of paedomorphosis, with mixed results. This is especially true for the *Pan* cranium, which has seen considerable attention over the last two decades. This attention includes finding evidence of paedomorphism in some aspects of the bonobo cranium (Lieberman et al. 2007; Williams 2001), while others believe that heterochrony does not play a role in shape differences between the two species (Mitteroecker et al. 2004; 2005). Finally, some have found evidence of peramorphism,

advanced ontogeny in descendant compared to ancestral species, in the endocranial ontogenetic trajectory (Durrleman et al. 2012). The aforementioned research has modeled developmental differences between *P. troglodytes* and *P. paniscus* using the entire cranium. While this approach makes intuitive sense, the cranium is made up of a number of different bones that may or may not have experienced independent changes in growth pattern. As a result of this and the equivocal findings of previous research, further work is needed on the ontogeny of the *Pan* cranium.

This study will address a gap in knowledge on morphology in *Pan* species by examining differences in frontal bone morphology in juveniles. Additionally, frontal bone ontogeny in bonobos will also be examined. In both analyses the entire frontal bone will be studied as well as the frontal squama, independent of the brow ridge. These methods were chosen primarily to test previous results and to reveal issues with the interpretations of those results. Specifically, it reveals the complexity of cranial ontogeny through the growth and interaction of cranial modules. The results will have important consequences for research which uses geometric morphometrics to study ontogeny and also for understanding *Pan* species' ontogeny as it relates to explanations for differences in phenotype between chimpanzees and bonobos, e.g. the self-domestication hypothesis (Hare et al. 2012).

CHAPTER 2: LITERATURE REVIEW

Section 2.1: Ontogenetic Trajectories and Heterochrony

Heterochrony has become a popular model for explaining phylogenetic divergence between ancestor and descendent populations. Interest in the topic has increased since Gould (1977), who described heterochrony as a mechanism for the link between ontogeny and phylogeny. Since Gould's work, heterochrony has had several different iterations (McNamara and McKinney 2005), but it is most currently defined as the changes in timing and/or rate of developmental events among ancestor and descendent individuals or taxa (Alberch et al. 1979; McNamara and McKinney 2005). Zollikofer and Ponce de León (2010) succinctly describe the form of an organism as a combination of its shape and size; size being affected by the growth of an organism, and shape affected by its development. Heterochronic analyses add the aspect of ontogenetic time onto these two parameters in an attempt to determine if there are shifts in the timing of development, separated from growth.

Heterochrony can be further distinguished by the type of transformation that occurs to the ontogenetic trajectory (Figure 1). Alberch et al. (1979) defined paedomorphosis and peramorphosis as "classes" of transformations in ontogenetic trajectories. Paedomorphosis refers to the retention of ancestral juvenile traits in a descendent species, while peramorphosis describes heterochronic transformations of descendent species which transcends, or grows past, the terminal point of the trajectories of the ancestral species. The authors describe different processes which can result in the development of paedomorphosis and peramorphosis. These processes include neoteny, acceleration, hypermorphosis, progenesis, post displacement, and pre displacement.

Neoteny, progenesis, and post displacement are all associated with paedomorphosis, while acceleration, hypermorphosis, and pre displacement are associated with peramorphosis. Neoteny and acceleration refer to a reduction or an increase in the rate of development respectively. Progenesis refers to the termination of an ontogenetic trajectory as a derived trait, while hypermorphosis is the extension of the trajectory past the ancestral termination. Finally, Alberch et al. (1979) describe post- and predisplacement as changes in the age at which a structure commences its ontogeny. Postdisplacement refers to the descendent species commencing development after the point in time in which ancestral species would begin development. Predisplacement is the beginning of development before that of the ancestral species. In addition to these transformations, Lieberman et al. (2007) adds postformation, preformation, rate hypomorphosis, and rate hypermorphosis. Postformation is paedomorphosis due to initial shape underdevelopment and preformation is peramorphosis due to initial shape overdevelopment.

Both paedomorphic and peramorphic transformations cause new phylogenetic features in descendent species. As a result, these transformations are described frequently in research concerning ontogenetic shape change. There have been many attempts at using these categories to understand morphological shape change throughout hominid evolution (Bruner et al. 2004; Bruner et al. 2013; Lieberman et al. 2007; Mitteroecker et al. 2004; Rice 2002; Williams 2001), and many researchers have hypothesized that heterochronic transformation played a major role in the evolution of the hominin brain and behavior (Jablonski et al. 2002; Leigh 2004; Penin et al. 2002), as well as the behavior of some great apes (Hare et al. 2012).

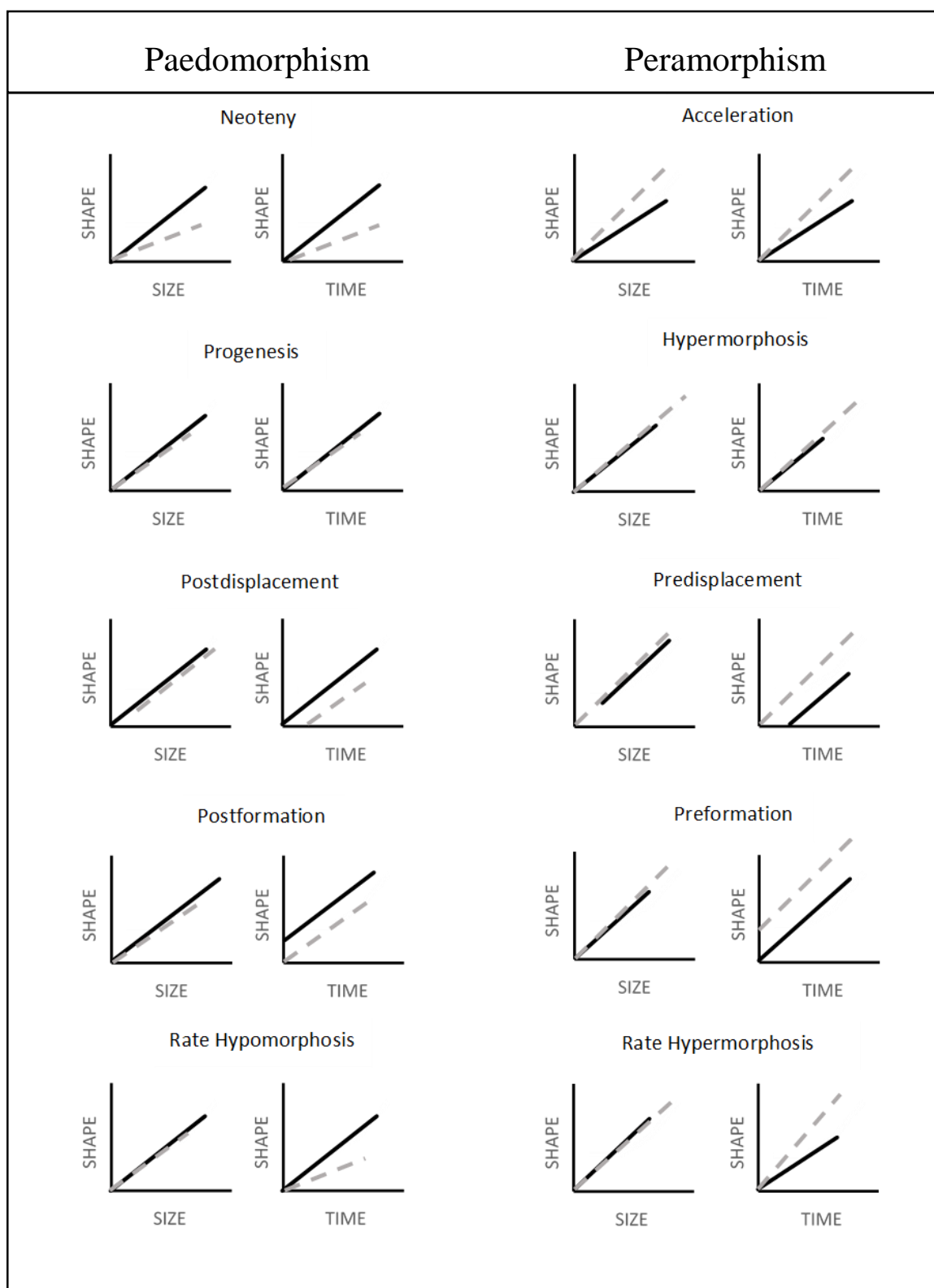


Figure 1: Models (after Alba 2002 and Lieberman et al. 2007) depicting heterochronic transformations during ontogeny. Solid black lines indicate the ancestral phenotype and the dashed grey lines indicate the descendant phenotype (after Alba 2002 and Lieberman et al. 2007).

Section 2.2: Geometric Morphometrics

Analysis of a morphological trait's ontogenetic shape change is typically conducted using geometric morphometrics, which are methods used to acquire, process, and analyze shape data (Slice 2005). Geometric morphometrics and more traditional morphometrics differ dramatically, due to the former's ability to retain all aspects of an object's geometric data. For geometric morphometrics, shape data can come in several different forms and the type of data are dependent on what is being studied and the type of results that are desired. For hominid crania, anatomical landmarks are typically the data used in shape analysis (Bruner et al. 2003; Bookstein et al. 1999; Lieberman et al. 2007; Mitteroecker et al. 2004, 2005; Williams 2001), although alternative types of data have been used. For example, Durrleman et al. (2012) examines morphological shape deformation by examining the position of data without selecting any data points and without assuming a relationship between said data points. Landmark data are typically recorded with 3D digitizers, computed tomography, and other imaging technology. The shape data are then processed and analyzed through the use of programs specifically designed for geometric morphometric function.

These programs analyze shape through a Procrustes superimposition, which is one of the most common methods used to understand shape. The Procrustes superimposition was first used by Kendall (1977; 1989) to determine if triplicate lithic monuments in Cornwall, England were collinear. Kendall developed a statistical method for analyzing the shape of the triangles, apart from their location and size. This procedure became a common method of shape analysis and has become a common tool for understanding biological variation in morphology. This analysis has been valuable in studies of hominid

ontogeny and development, as more traditional morphometrics fail to make use of all the geometric data available in a data set and have certain limitations that do not affect geometric morphometric procedures (Adams et al. 2004; Slice 2005).

The Procrustes superimposition scales and configures the data, which allows for an interpretation; namely, examining trends in shape variation, comparing sample means, and assessing symmetry to name a few. Procrustes superimposition separates out the shape from the non-shape data, i.e. location, orientation, and size. Shape data are isolated by translating, scaling, and rotating the landmarks to a reference, which is typically the mean shape of the sample scaled to centroid size (Slice 2005). The superimposition estimates the optimal scale, orientation, and location for each configuration that results in the lowest least-squares distance from the mean. This is done for each observation and the result is a sample where non-shape factors are removed. In addition, the centroid size for each configuration is created in the superimposition by calculating the summed squared distance from the landmarks to the centroid of the configuration (Slice 2005). As such, it acts as a good measure for the size of a structure and changes in size through ontogeny.

After the data have been transformed through a Procrustes superimposition, the ontogenetic shape change can be visualized through a principal components analysis (PCA). The PCA creates variables based on the dimensions of shape variation in a sample. These dimensions are ordered based on the amount of variance they explain. The changes in shape that occur in the sample for each dimension/variable can be visualized by creating a regression of two or more principal components (Mitteroecker et al. 2005; Lieberman et al. 2007), creating an allometric analysis. It can also be done by setting a

single principal component (PC) against a measurement of timing, such as chronological age or dental eruption (Lieberman et al. 2007). It should be noted, however, that while PCs do explain shape change in a cross-sectional, statistical sense, they are not created through analyses of biological shape change. As a result, any interpretations of PC shape change must be made with the understanding that they are not true measures of shape change during ontogeny.

Past research has attempted to pair the types of heterochrony with slopes and intercepts of the aforementioned types of analyses (Alberch et al. 1979; Alba 2002; Lieberman et al. 2007). Ancestral and descendent ontogenetic trajectories are compared in order to assess the heterochronic transformations that may have occurred to the ontogeny of the descendant. Simplified, the analyses typically present the trajectory of descendant species terminating before the ancestral trajectory in pedomorphosis and terminating after in the case of peramorphosis. The y-intercept also plays a role in cases such as post- and pre-formation and post- and pre-displacement.

These methods for interpreting PCA to make inferences about ontogeny and heterochrony have been debated in recent research. Mitteroecker and colleagues (2005) argue that the only way pure heterochrony can occur is when the ontogenetic trajectories of the two species directly overlap when visualizing ontogeny trajectories through allometry. The only heterochrony detectable between the trajectories would come in the form of extension or truncation of the trajectory itself, indicating that descendent development ceased before or extended past the development of the ancestor. Additionally, this can only occur when the study is multivariate, i.e., using more than two PCs. The authors show how a plot depicting shape change through two PCs can be

erroneous as a result of the two dimensional nature of the plot. If a third dimension, through the addition of a third PC, is added onto the plot and the view of the plot is rotated, it can be seen that two trajectories' relationship can change depending on viewing position, e.g. divergent trajectories can appear parallel depending on the position. Using a multivariate analysis is believed to counter this problem and determine if heterochrony occurred. Lieberman et al. (2007) dispute this claim and suggest that multiple PCs are not needed because species which have the exact same ontogenetic trajectory would be identical in their shape change regardless of how many PCs were analyzed. It is expected that closely related, but divergent species would vary in their ontogenies. As such, having only a single PC show similar, but not exactly aligned trajectories, is still evidence of heterochrony. In fact, Lieberman et al. (2007) claim that it is a good measure of the degree of covariation in ontogeny between species.

Lieberman et al. (2007) also state that previous studies of heterochrony in the *Pan* species did not test directly for paedomorphism because they did not examine the ontogenies through time, but rather used growth as a proxy; this method creates an allometric analysis. Allometry examines the shape change that occurs during growth, i.e. size change. Heterochrony examines the changes in rate/timing of developmental events. Allometry does not allow for direct inferences about temporal aspects of developmental shifts; as a result, heterochronic transformations may not be visible in allometric trajectories. A relative measure of age, such as dental eruption, should be used rather than growth as it allows for the temporal aspect required to view shifts in developmental timing. Seselj (2013) offers a counterargument to using dental development. The author found that the relationship between dental development and skeletal growth to be

moderate at best. They cautioned against associating advances in dental development with advances in skeletal growth.

Finally, modularity is an important concept to understand when examining ontogenetic trajectories for heterochrony. A module is defined as “a unit that is tightly integrated internally but relatively independent from other such modules” (Klingenberg 2008). An organism’s modules are determined at the cellular level, with the body made up of many modules that each have their own genetic instructions for growth and development. These modules are the building blocks for allometric growth and heterochrony, as changes to the modules in size, developmental timing, and growth will likely cause changes to the growth and development of the structure as a whole. McCollum (1999) provides an excellent example of how module growth can alter the morphology of structures. The author refutes earlier studies that attribute robust australopithecines to a common monophyletic origin based on multiple craniodental features. She states that many of the cranial traits claimed to be synapomorphies are actually the result of dental growth and development. The morphology of the face is altered through development of key aspects of the dental structure and their displacement/interaction with other structures of the face. This results in a cranial morphology that appears to be common among different species of australopithecines, when in reality only a few select traits are similar. McCollum’s (1999) work provides an excellent example of how modularity functions in the morphology of a structure and how different modules can affect each other.

It is unlikely that a single global event, such as growth hormone over-expression or early cessation of growth, can cause a single heterochronic transformation to occur in a

structure over multiple modules. More likely, what is occurring is dissociated heterochrony. That is, each growth field has a separate ontogenetic trajectory (Mitteroecker et al. 2005). In order to combat error introduced by multiple, interacting, heterochronic fields, researchers have focused on studying the ontogenetic trajectories of modules rather than global elements. While this may reduce the chance of analyzing multiple growth fields, it is important to acknowledge that modules are not completely discrete units (Klingenberg et al. 2003). This fact warrants further study of the cranium, as past work (Lieberman et al. 2007) has failed to take this interaction into consideration.

Section 2.3: Results of Past Work with Chimp and Bonobo Heterochrony

Chimpanzee and bonobo cranial ontogeny has had considerable attention in recent years. Past research has found that the two species diverged approximately 2 million years ago (Horai et al. 1992), with more recent analyses finding the divergence closer to 1 million years (Hey 2010). Currently, there is no morphological evidence for the last common ancestor of chimpanzees and bonobos, but some researchers have noted that chimpanzee ontogeny more closely resembles gorilla ontogeny, suggesting that their development is more ancestral (Shea 1983; Wrangham and Pilbeam 2001). While not direct evidence of the last common ancestor, these suggestions do warrant further study and provide evidence in support of bonobo pedomorphism.

A number of publications have attempted to determine if bonobo crania are pedomorphic to chimpanzees. Shea (1983) represents one of the earliest studies that hypothesized that bonobos were pedomorphic, or scaled, versions of chimpanzees. By examining body dimensions of chimpanzees and bonobos during ontogeny, Shea found that the differences between the two species are due to an ontogenetic scaling. He argued

that bonobo features are formed by a termination of the ontogenetic trajectory observed in chimpanzees, with the former retaining juvenile traits into adulthood. Other studies have found that chimpanzee and bonobo infant and prenatal crania carry many morphological similarities (Williams 2001; Minugh-Purvis et al. 2002), to such a degree that some researchers have claimed that the two apes typically resemble each other pre- and post-natally (Schultz 1924; Richtsmeier et al 1993; Richardson 1999).

Geometric morphometrics have been employed to examine shape and size differences in the hopes of finding evidence of paedomorphic transformation to bonobo ontogeny. Williams (2001) compared craniofacial shape between modern humans, Neandertals, chimpanzees, and bonobos. Williams claims that due to differences in development during the ontogeny, the initially divergent morphologies of chimpanzees and bonobos appear to realign throughout ontogeny. Due to this, the research argues that there are more craniofacial shape differences within each species' development than between the two species at comparable ages; but bonobo development does not terminate at a point of pre-adult development in chimpanzees, which is an argument for paedomorphism. The author argues that these results suggest that bonobos do not have a weaker growth allometry and thus neoteny is not a factor in bonobo growth. From his results, Williams infers that only slight paedomorphic heterochrony was found in the calotte and thus an ontogenetic shift can only explain a portion of bonobo evolution.

Mitteroecker et al. (2005) reject earlier work on chimpanzee and bonobo ontogeny due to issues with methodology. As an alternative to earlier work, they examined chimpanzee and bonobo ontogenetic trajectories at the global and regional levels with multiple principal components. Regional levels included the neurocranium,

upper face, and lower face. An analysis of the first three principal components suggests the two species differ in ontogenetic trajectories, even at the earliest ages. Both global and regional analyses reveal that there are different trajectories for the two species. Based on this, the authors claim that heterochrony cannot explain the differences between chimpanzee and bonobo crania.

Lieberman et al. (2007) assess bonobo paedomorphism through geometric morphometric methods similar to Mitteroecker et al. (2005). Unlike previous work, they examine landmarks on both the external and internal tables of the cranium. They also assess the relative age of each specimen and examine the species' shape changes across life stages for reasons stated earlier. This work included testing of two hypotheses: the first states that the entire bonobo skull is paedomorphic, and the second hypothesis states that the facial and neurocranial regions are distinct and only a part of the bonobo skull is paedomorphic. The first PC for the cranium as a whole, the neurocranium and basicranium (NBC), and the face were plotted against estimates of age, including dental eruption and centroid size, in a regression. The results for the whole cranium indicate similar slopes but significantly different intercepts. The authors argue this indicates that the species have similar trajectories but that the bonobo is underdeveloped likely due to post-displacement. Similar results occurred for the face, but to a much weaker degree. Based on this, the authors conclude that they cannot determine if the bonobo face is paedomorphic compared to chimpanzees. Finally, analyses of the NBC reveals that a regression with dental age estimates leads to a significantly different intercept but not slope. On the other hand, a regression with centroid size reveals no significant difference in slope or intercept. The authors claim that the NBC is likely paedomorphic via post-

displacement based on these results. In summation, the authors believe that paedomorphism can explain some, but not all, aspects of shape difference seen between chimpanzees and bonobos.

Interestingly, another study of chimpanzee and bonobo cranial ontogeny examines the endocranial surface as a proxy for brain growth and development (Durrleman et al. 2012). The study focuses on the ontogeny of the *Pan* species using dental development stages. Comparisons of chimpanzee and bonobo endocranial surfaces reveal a distinct difference in ontogenies. Bonobos show a rapid endocranial expansion in the frontal, parietal, and occipital areas before the emergence of the first permanent molars. Subsequent to eruption of the molars, there is a significant ($P < 0.05$) slowdown in growth. On the other hand, chimpanzees show a much slower rate of expansion that is in line with the dental development, with the brain expanding during the eruption of the deciduous and adult molars. Endocranial volume also differs drastically between the species, as bonobos see a relatively rapid increase in capacity early in development while chimpanzees see a more gradual increase in capacity. It appears that the bonobo brain has accelerated development compared to the chimpanzee, but the authors agree that bonobo ontogeny cannot be described in single terms of heterochrony. Regardless, there is a distinct difference in ontogeny of the brain between the two species.

Clearly there is considerable debate concerning the topic of heterochrony and the bonobo cranium. The complexity of modular growth and the influences and interactions that occur between growth fields make identifying the ontogenetic trajectories of structures difficult. Additionally, the variation in morphology between the two species may also be due to different evolutionary forces acting on the two species in the 1 to 2

million years since their divergence. Heterotopy, or the movement of structures over evolutionary time, also results in new phenotypes. Hall (2002) uses the movement of internal pouches in geomyoid rodents and the movement of portions of the jaw during the formation of the inner ear in mammalian evolution as examples of how heterotopy can cause variation in morphology. These factors may be responsible for the different results seen from past work. It may also, in part, be due to the relatively recent development of the methods used to compare the shapes of the crania.

CHAPTER 3: RATIONAL FOR RESEARCH

The study of heterochrony in *Pan* species is important for understanding the evolutionary divergence between chimpanzees and bonobos, as well as for understanding the large differences in behavior witnessed between the two species. Bonobo paedomorphism is a vital and involved part of the self-domestication hypothesis proposed by Hare et al. (2012). Their argument for the differences between chimpanzees and bonobos is based on sexual selection against aggressive behavior. This selection against aggression targets genes that affect neuroendocrine maturation, leading to more juvenile forms of behavior. Traits that were not directly selected for but were still under the influence of these genes are also affected by this sexual selection. This results in bonobos having both paedomorphic behavior and morphology, along with other juvenile features. This argument is based on a large amount of prior research which found the presence of paedomorphism in bonobo behavior and morphology. These past investigations found evidence of juvenility in aspects of external appearance and body size (Kano 1992), endocrine function (Behringer et al. 2014), and social behavior and cognition (Rosati and

Hare, 2012; Wobber et al. 2010). Hare et al. (2012) also cite cranial juvenility as one source of evidence for paedomorphic morphology. In truth, bonobo cranial paedomorphism is complex and past research has only found slight paedomorphosis, and only in certain elements. In addition, evidence of peramorphosis has been detected in studies of the bonobo endocranial surface (Durrleman et al. 2012). Paedomorphism and paramorphism are not mutually exclusive in a structure and, in fact, this is argued to be evidence of a system of trade-offs, as an accelerated growth in one area is paid for energetically by reduced growth in other areas (McNamara 2002). As a result of this complexity in growth and the conflicting results of previous studies, further work is needed on the growth of *Pan* crania in order to assess its use as evidence for the self-domestication hypothesis (Hare et al. 2012).

This research seeks to continue examination of *Pan* cranial ontogeny by expanding on earlier studies of *Pan* species' cranial ontogeny, with the hope of refuting earlier work. It is believed that previous work failed to fully consider the effects of interaction on the different regions of the cranium. This resulted in an oversimplification of their interpretations concerning bonobo ontogeny. As a result, this research will have two separate goals: to test the validity of methodology used in past work by altering the procedures slightly and to provide evidence which will support or refute past results regarding the ontogeny of chimpanzees and bonobos seeks to test past results and interpretations of the relationship between modules of the cranium and claims of heterochrony in certain regions. In order to achieve these goals, this research will study aspects of chimpanzee and bonobo cranial morphology and bonobo cranial ontogeny by focusing only on the frontal bone of the cranium. This is an alteration to past

methodology which examined heterochrony in the entire cranium or in regions, i.e. neurocranium and basicranium (Lieberman et al. 2007; Mitteroecker et al. 2005; William 2001). While the authors of these studies attempted to account for modularity, dissociated heterochronic fields may have still had an effect on their results. By examining the frontal bone, the risk of analyzing multiple fields is reduced.

The frontal bone was chosen due to its inclusion in the neurocranium and due to its proximity to the face. While the frontal is a part of a module in the neurocranium (Goswami 2006), it has never been studied as an independent unit. Studying the bone by itself may reveal important ontogenetic information concerning heterochrony and modular interaction that was not revealed when entire modules were the focus of study.

The frontal bone was also chosen due to substantial morphological changes that occur during the ontogeny of the cranium. The development of prognathism and post-orbital constriction during ontogeny significantly change the morphology of the frontal bone and make it an excellent subject of study for comparisons of shape change in the species. Additionally, research on the *Pan* species' frontal bone may have important consequences for hominin evolution and paleoneurology, as the shape of the hominin frontal bone changes dramatically throughout human evolution

In addition, shape change of the frontal squama will be analyzed apart from the browridge. Bruner et al. (2013) suggested that the squama and browridge are affected by different influences and have separate structural roles. While the shape of the squama is largely influenced by the brain, the brow acts as a barrier between the face and neurocranium and is likely formed as a result of facial projection anteriorly to the neurocranium, rather than due to biomechanical stress (Athreya 2009; Bruner et al. 2013;

Lieberman 2000). As a result Bruner et al. (2013) claim that the two elements should be studied independently. For this study, the ontogeny of the frontal, in its entirety, and the squama will be both analyzed in order to examine shape variation of the frontal, and to determine the shape variation of the squama, separated from influences that may be affecting the shape of the browridge.

CHAPTER 4: MATERIALS AND METHODS

Section 4.1: Sample and Landmarks

The data for this study came from a collection of 61 *Pan paniscus* and 28 *Pan troglodytes* crania, located at the Royal Museum for Central Africa in Tervuren, Belgium. Frontal bone landmarks from the 89 crania were digitized with the use of a Microscribe 3dx digitizer. The digitizer was chosen for the acquisition of the data due to the ability of the digitizer to quickly collect the data, and the flexibility of the data output after collection. The microscribe collected data in 3-dimensional space and then output the data into a spreadsheet with the x, y, and z coordinates. A total of 10 landmarks located on the frontal bone were recorded using the digitizer. These landmarks include the nasion, bregma, glabella, left and right pterion, left and right frontomale junctions, the midpoint between the nasion and bregma, and the left and right midpoints between the bregma and pterions (Figures 2 and 3). The sample consists of male (n=21), female (n=22), and unidentified (n= 37) specimens, ranging in development from infant to adult.



Figure 2: 3D image of a *Pan paniscus* specimen from the collection at the Royal Museum for Central Africa.

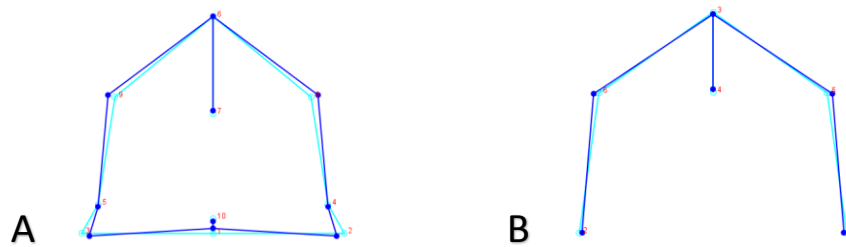


Figure 3: (A) is a wireframe including the landmarks: nasion, bregma, glabella, left and right pterion, left and right frontomale junction, the midpoint between the nasion and bregma, and the left and right midpoints between the bregma and pterions. (B) is a wire frame including the landmarks: bregma, left and right pterion, the midpoint between the nasion and bregma, and the left and right midpoints between the bregma and pterions.

Section 4.2: Aging

Age of the specimens was assessed through dental development, similar to earlier studies of *Pan* species' ontogeny (Mitteroecker et al. 2005; Lieberman et al. 2007; Durrleman et al. 2012). Relative age was determined by the eruption of permanent dentition, based on work done by Zihlman et al. (2004). The study focused on dental eruption in wild chimpanzees, with eruptions associated with the life stages of infant, juvenile, adolescent, and adult (see Table 1). Zihlman et al. (2004) described the eruption of the M1 as the cessation of infancy and the beginning of the juvenile life stage. This occurs at approximately 4 years of age. The juvenile life stage lasts from approximately age 5 to age 10. During this time, I1, I2, and M2 emerge. The eruption of the canines at approximately 10 to 11 years of age is associated with the beginning of the adolescent life stage. Zihlman et al. (2004) state that the M3 erupts before chimpanzees reach behavioral adulthood, at approximately the age of 12.5 years. Through analysis of the sample's dental development it became apparent that none of the specimens fell into the adolescent category. As a result, age estimates will only consist of 3 life stages associated with dental development: infancy, juvenility, and adulthood (Table 2).

As noted in Lieberman et al. (2007) the study of bonobo growth and development has suffered from a lack of research into dental development. The studies that do exist claim that bonobo dental development falls within the range of dental development in chimpanzees, albeit towards the lower range of variation (Smith et al. 1994; Boughner and Dean 2004). As a result, this study assumed that both chimpanzees and bonobos fall under the same dental eruption and life stage pattern. At the very least, the sequence of

eruption is the same in both species, which allowed them to also be classified into the 3 life stages.

Table 1: Table depicting the growth stages of the Pan species, with corresponding dental development and life history events that correspond with the dental development.

Growth Stage	Infant	Juvenile	Adolescent	Sub-Adult
Chronological Age in years	0 to ~4	~5 to ~10	~10 to ~12	~12
Dental Eruption	Deciduous	M1, I1, I2, M2	Canines	M3
Significant Developmental Events	Infant growth period	Cessation of brain growth	Adolescent growth period	Beginning of cessation of growth

Table 2: A cross-tabulation of the sample by species and life.

Species	Infant	Juvenile	Sub-Adult	Grand Total
<i>troglodytes</i>	3	21	2	26
<i>paniscus</i>	13	38	3	55
Grand Total	16	59	5	80

Section 4.3: Sex

Sex of each specimen, when known, was included in the inventory list of the collection. As approximately half of the sample had a sex designation, and removal of unassigned specimens would severely limit the analysis, it was deemed important to assess whether sex played a role in shape variation of the frontal between and within species.

Table 3: A cross-tabulation of the sample by species and sex. Unidentified specimens did not have a sex designation.

Species	Male	Female	Unidentified	Grand Total
<i>trogloodytes</i>	5	10	11	26
<i>paniscus</i>	16	12	26	55
Grand Total	21	22	37	80

Section 4.4: Geometric Morphometric Methods

Investigation of the digitized frontal bone was carried out through the use of geometric morphometric shape analysis. This analysis was carried out by the MorphoJ© software package (Klingenberg 2011). Initially, the data created from the Microscribe digitizer was saved as a tab-delimited text file in order to fit the required format for the MorphoJ program. The MorphoJ program requires the individual specimens to be listed in single column, with the landmark coordinates listed after the specimen in each row (e.g. specimen x y z). This required the removal of classifier data, i.e. age, sex, and species. Fortunately, the classifier variables were reinserted into the data after it had been loaded into the program.

Before the Procrustes superimposition and PCA were carried out a new dataset was constructed from the frontal landmarks to be used in addition to the frontal. The new dataset consisted of the bregma, left and right pterion, the midpoint between the nasion and bregma, and the left and right midpoints between the bregma and pterions (Figure 3B). A Procrustes superimposition and a principal component analysis were performed on both the original dataset (frontal) and the new dataset (squama). Additionally the centroid size and log-transformed centroid size values were constructed for each

specimen. After which, the principal component scores for both datasets, centroid size values, and classifiers were exported into R 3.1.1 for the correlation tests and SPSS version 22 for the ANCOVA.

Additionally, the PCs were assessed to determine if the scores were correctly aligned with ontogeny. With a PCA, the sign of PC scores is arbitrary, only the values' relation to each other is important for shape change analyses (Singleton 2005). As a result, PCs can appear to be negatively correlated with ontogeny. This can be rectified by reversing the PC scores to correctly align the shape data with centroid size and life stages, this is done by multiplying the PC scores by -1.

Section 4.5: Statistics

After the PC scores were created and correctly aligned with measures of growth the data were statistically analyzed. Throughout the statistics, an α -level of 0.05 was used as the threshold to indicate significance for all tests. Standard descriptive statistics were obtained and Pearson's Chi-square tests were run on the categorical variables. The PC scores are arbitrary values that have no meaningful information outside of their relation to each other. As a result, a statistical summary of each PC does not provide useful information.

Specimens were removed from the dataset if they varied drastically from the average shape of the sample. Specifically, z-scores were calculated by centroid size and specimens who were at or approaching 3 or -3 were removed from the sample.

In both the frontal and squama datasets, the R statistical package was used to assess which PCs correlated with centroid size, as an estimate of age. The PC scores

which had a significant correlation with centroid size ($P < 0.05$) between the two species were then tested in an ANCOVA using SPSS (version 22). Due to the limitation of inadequate sample size for infants and adults the correlation tests and ANCOVA were run with only the juvenile specimens for the comparison of morphology at this stage in development. Significant PC's were then plotted against log centroid size and were assessed based on previous work's heterochrony models (Alba 2002; Lieberman et al. 2007).

In order to counteract the limitations brought on by only comparing juveniles between species, bonobo infants and juveniles were plotted against log centroid size and life stage in order to get a proper ontogenetic trajectory. The ontogenetic trajectory was limited to infant and juvenile bonobos due to the fact that the other categories: bonobo adults, chimpanzee infants, juveniles, and adults, had limited sample size and did not adequately represent the shape variation that would occur. This visualization was done in order to assess how age was affecting shape change, resulting in information on the rate of development during a large portion of bonobo growth.

CHAPTER 5: RESULTS

Section 5.1: Descriptive Statistics

The log centroid size values for each dataset, i.e. frontal juveniles, frontal infant and juvenile bonobos, squama juveniles, squama infant and juvenile bonobos, is provided (Table 4). While centroid size and log centroid size had a comparable effect on the data,

it was decided that log centroid size would be a better measure of growth due to the fact that it better encompassed the large amount of shape variation in the sample.

Table 4: Descriptive statistics for log centroid size for the different data sets used in this study.

Dataset	n	Mean	Standard Deviation	Range (Minimum)	Range (Maximum)
Frontal- Chimpanzee Juvenile	21	4.76603	0.03542626	4.699046	4.824218
Frontal- Bonobo Juvenile	38	4.703911	0.05158878	4.613292	4.835009
Frontal- Infant and Juvenile Bonobo	51	4.676234	0.07408794	4.444474	4.835009
Squama- Chimpanzee Juvenile	21	4.434645	0.0247911	4.373452	4.473498
Squama- Bonobo Juvenile	38	4.392433	0.0507294	4.32055	4.613762
Squama- Infant and Juvenile Bonobo	51	4.373349	0.06418653	4.150291	4.613762

Chi-Square results for species and life stage was not significant ($P = .431$), although the assumption of minimal cell frequencies was not met. 2 cells (33.3%) had an expected count of less than 5. The Chi-Square results for sex and life stage was also not significant ($P = .996$), but likewise violated the assumption of expected frequencies with 4 cells (66.7%) having an expected count of less than 5. While the violation of the assumption is a limitation of this study, the results of the Pearson Chi-Square test indicate that the categorical variables are not significantly associated.

Finally, analysis of centroid size z-scores revealed that 9 of the 89 specimens in the sample reached or approached a z-score of 3 or -3. These individuals were removed from the sample.

Section 5.2: Frontal Bone with Browridge

The principal component analysis created and ordinated a number of shape variables based on the amount of variance that each variable explained. Results of the analysis revealed that the PC1 explains 43.7 % of the total variance in shape. The rest of the variance was explained by 12 other PCs, see Table 5 for a breakdown of each PC. In regards to chimpanzee and bonobo juveniles, PC1 was the only PC that was significantly correlated between and within the species. For the sample containing infant and juvenile bonobos PC1, PC6, PC8, and PC11 were all significantly correlated with log centroid size, but it was determined that PC6, PC8, and PC11 should be excluded based on the low amount of shape variation that they explained (Table 5). As a result, PC1 was the only PC used to compare species' means and to analyze and visualize the bonobo ontogenetic trajectory (Table 6).

The effect of sex on shape variation was tested through the use of a Mann-Whitney U test. Results indicated that PC1 did not significantly differ between males and females ($P=.544$). As a result, the sample was pooled independent of sex.

Wireframes were used to depict the shape change that is represented by the PC1 scores (Figure 4). Shape change for PC1 appears to be primarily occurring in the browridge. Lower PC values represented a smaller browridge while higher PC values represented a widened and enlarged browridge. Considering that size is controlled for, these shape changes were congruent with what would be expected to occur during *Pan* cranial growth.

Table 5: PCA results for the frontal bone.

PC	Eigenvalues	% Variance	Cumulative %
1.	0.00359199	43.700	43.700
2.	0.00118919	14.468	58.168
3.	0.00085422	10.392	68.560
4.	0.00068775	8.367	76.928
5.	0.00060290	7.335	84.263
6.	0.00035925	4.371	88.633
7.	0.00027828	3.386	92.019
8.	0.00022962	2.794	94.813
9.	0.00018129	2.206	97.018
10.	0.00013791	1.678	98.696
11.	0.00005780	0.703	99.399
12.	0.00002762	0.336	99.735
13.	0.00002177	0.265	100.000

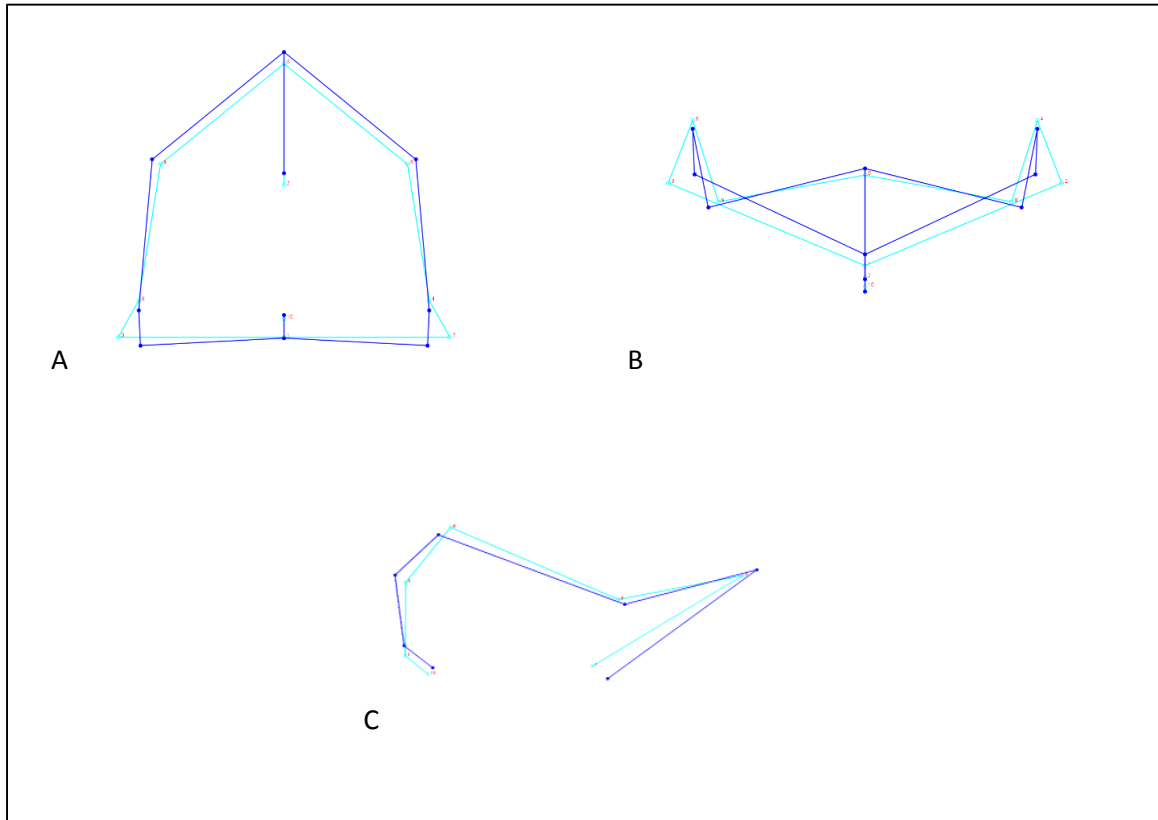
Table 6: Table 6: A list of the PCs used in this study which were significantly correlated with log centroid size.

*- PC was dropped from the analysis due to the extremely low amount of variance that each explained.

Dataset	Sample	PC	r	Sig.
Frontal	Juvenile chimpanzee	PC1	0.72	0.00013
Frontal	Juvenile bonobo	PC1	0.53	0.00034
Frontal	Inf. And Juv. bonobo	PC1	0.61	9.053×10^{-7}
Frontal	Inf. And Juv. bonobo	PC6*	0.24	0.047
Frontal	Inf. And Juv. bonobo	PC8*	0.59	2.372×10^{-6}
Frontal	Inf. And Juv. bonobo	PC11*	0.27	0.02633
Squama	Juvenile <i>Pan</i>	PC1	0.30	0.01076
Squama	Juvenile <i>Pan</i>	PC3	0.32	0.006275
Squama	Juvenile <i>Pan</i>	PC6*	0.31	0.008623
Squama	Inf. And Juv. bonobo	PC3	0.44	0.0005793

The ANCOVA of PC1 for the comparison between juvenile chimpanzees and bonobos revealed that there is a significant difference between species ($P = .000$) while controlling for log centroid size ($P = .000$). Additionally, the ANCOVA revealed that there was significant interaction ($P = .007$) between the covariate log centroid size and species. These results indicate that there is not only a significant difference between the two species in respect to PC1, but also the significant interaction suggests that the relationship between PC1 and log centroid size differs between the two species (see Figure 5).

The ANCOVA of PC1 for bonobo infants and juveniles revealed that there was not a significant difference between life stages ($P = .109$) for PC1 while controlling for log centroid size ($P = .000$). Additionally, the interaction between life stage and log centroid size was significant ($P = .026$), indicating that the two variables may be explaining the same variance. It also suggests that the relationship between PC1 and log centroid size differs by life stage. A plot of PC1 against log centroid size with life stage showed a lesser slope for infants and a greater slope for juveniles (Figure 6). This was indicative of a rate of development which was slower in infancy and quicker once the bonobo reached a juvenile age, usually associated with the eruption of the 1st adult molar.



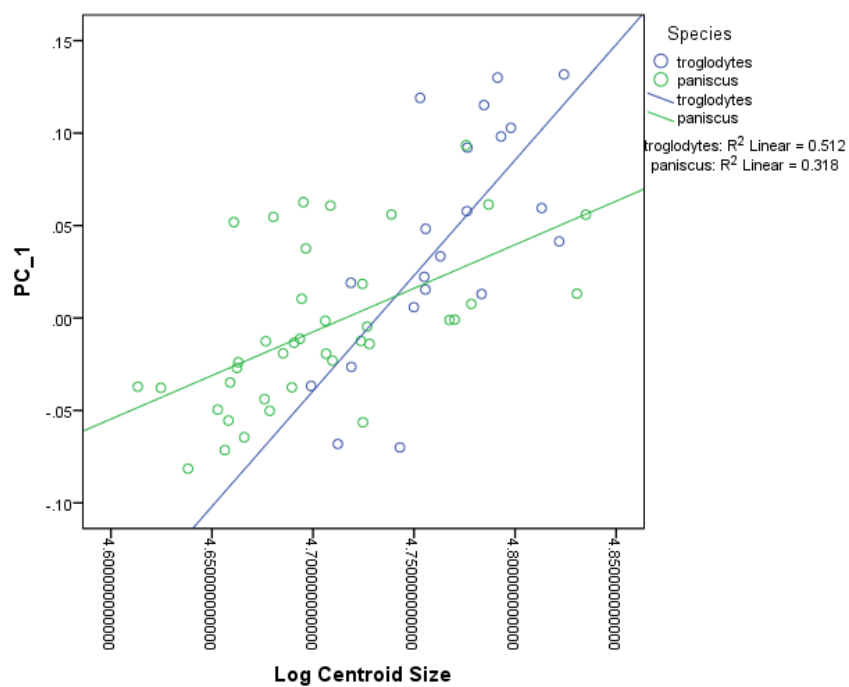


Figure 5: Plot of frontal PC1 vs. log centroid size with specimens grouped by species.

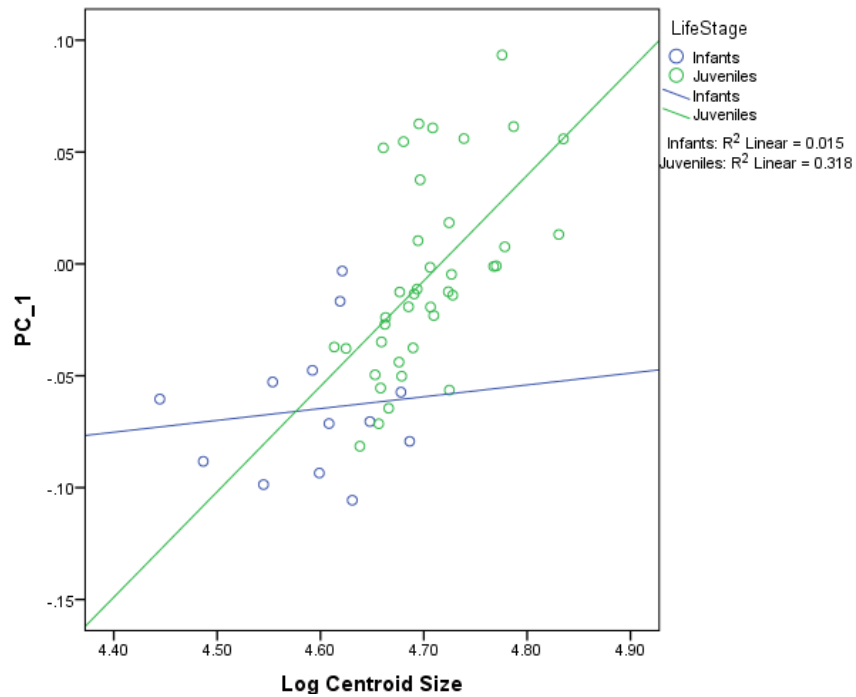


Figure 6: Plot of frontal PC1 vs. log centroid size with specimens grouped by infant and juvenile life stages.

Section 5.3: Frontal Bone without Browridge (Squama)

The PCA of the squama data created 6 shape variables (see Table 7 for a list of the PCs and the amount of variance that is explained by each). In regards to the comparison between chimpanzee and bonobo juveniles, no PCs were significantly correlated with log centroid size. As a result, correlation tests were run on the two species as a single sample. Results indicate that PC1, PC3, and PC6 were all significantly correlated with log centroid size, although PC6 was dropped due to the fact that it explained less than 2% of the variation in shape (Table 7). In regards to infant and juvenile bonobos, PC3 was the only PC correlated with log centroid size (Table 6). Similarly to the PCs for the frontal, a Mann-Whitney test found that PC1 ($P = .584$), and PC3 ($P = .130$), were not significantly different between males and females; as a result, the samples were pooled for the analysis.

Table 7: PCA results for the squama.

PC	Eigenvalues	% Variance	Cumulative %
1.	0.00173815	48.564	48.564
2.	0.00063907	17.856	66.420
3.	0.00061141	17.083	83.503
4.	0.00028190	7.876	91.380
5.	0.00023766	6.640	98.020
6.	0.00007087	1.980	100.000

ANCOVA analyses of PC1 and species with log centroid size reveal that there was not a significant difference between the two species ($P = .205$) for PC1 when controlling for log centroid size ($P = .185$). Additionally the interaction between species and log centroid size was not significant ($P = .966$).

Analysis of PC3 and species with log centroid size revealed that there was not a significant difference between the two species ($P = .113$) for PC3 when controlling for log centroid size ($P = .000$). Additionally, there was not a significant interaction ($P = .293$). This indicates that there is no significant difference between the two species in the growth of the squama that is represented by PC1 and PC3, though size change was a significant predictor of PC3.

In regards to the analysis of the bonobo ontogenetic trajectory, although PC3 does correlate with log centroid size, an ANCOVA of PC3 and life stage, with log centroid size as a covariate, shows that there was not a significant difference between life stages ($P = .103$) in regards to PC3. Additionally, the interaction of life stage with log centroid size is also not significant ($P = .122$), ruling out covariance. While log centroid size is a predictor of PC3 ($P = .003$), there is not enough shape change throughout ontogeny for there to be a difference between infants and juveniles.

CHAPTER 6: DISCUSSION

These results raised important questions about previous findings concerning *Pan* morphology and ontogeny with the use of geometric morphometric methods. The comparison of juvenile chimpanzee and bonobo frontal bones through an ANCOVA revealed that the two species differ in shape for some aspects of development (PC1) during the juvenile life stage. Additionally, the significant interaction between the covariate and the predictor variable indicated that the two regressions, representing the species of *Pan*, had different slopes (Figure 5). It is speculated that these differences indicate divergent trajectories, suggesting that heterochrony is not a factor in the

development of the bonobo frontal bone, although further work is required to verify this claim.

In contrast with the results of this study, Lieberman et al. (2007) found evidence of paedomorphism in the neurocranium. Based on these results, the authors suggested that the neurocranium and face must be at least partly dissociated ontogenetically due to fact that the face was not paedomorphic. Past research supports that the browridge is formed as a result of the face projecting past the rest of the cranium (Lieberman 2000). Other work (Mitteroecker and Bookstein 2008) has found that the face and neurocranium share several common shape factors. These findings argue that regions of the frontal are formed and influenced by interaction with the face. The results of this study support that a portion of the neurocranium, i.e. the frontal bone, also has divergent trajectories between chimpanzees and bonobos. This shape change appears to be focused in the browridge, as revealed by the visualization of PC1 for the entire frontal. Based on the findings of past work, it is argued that this shape change is caused, in part, by an interaction with the face. These findings are contradictory to the claims of dissociation made by Lieberman et al. (2007) and indicate that the neurocranium's ontogeny cannot be absolutely defined as paedomorphic.

These findings reveal that the ontogeny of the cranium is a complex progression that cannot be explained by a single heterochronic transformation. Past work attempted to assess the ontogeny of entire modules in the cranium, without consideration of the interactions that could occur between modules. The current study's model, evaluation of a single bone rather than an entire module, revealed the complexity of shape change that could occur within a single bone. It is suggested that this model provides a finer degree of

analysis for ontogeny and should be used to test for heterochrony. This could also assist in detecting potential influences between the bones of the cranium. For example, a comparison between the frontal and parietal bones may reveal that the lack of shape change in the squama may coincide with rapid shape change in the parietals. This could reveal information on the interactions between even the individual bones of the cranium.

As a result of these findings, the current argument for paedomorphic cranial morphology in the self-domestication hypothesis (Hare et al. 2012) warrants further study. Past work based on experiments with fox domestication noted distinct changes to cranial morphology, including a shortening and widening of the face and a general decrease in size for males (Trut et al. 2004). Based on these morphological transformations during domestication, Hare et al. (2012) suggested that the bonobos apparent juvenilized characteristics, citing Lieberman et al. (2007), are a product of self-domestication. The results of this study and the findings of other work (Durrleman et al. 2012; Mitteroecker et al. 2005; Mitteroecker and Bookstein 2008) do not support the claims of a juvenilized cranial morphology in bonobos and it is suggested that this claim be reassessed in light of these more recent findings. The shape changes witnessed in domesticated fox crania occurred relatively rapidly, over several generations in a 40 year period. It is likely, if self-domestication did occur for bonobos, that cranial shape change would have been rapid as well. Considering the two species diverged approximately 1-2 million years ago, other factors may have also influenced the shape and size of the crania. Thus, it is not likely that the rapid changes to morphology caused by the self-domestication of a species could be detected apart from other evolutionary forces during the species evolution.

The analysis of bonobo shape change through ontogeny, grouped by life stage, indicated that development does occur at different rates of time for the different life stages. Visualization of the group slopes revealed that there is a slower rate of development for infants and a more rapid rate of development for juveniles in regards to the aspects of the frontal represented by PC1 (Figure 6). This suggests ontogeny is not linear and the rate of development for the frontal increases as the bonobos age, similar to general somatic growth. It is assumed that the rate of development decreases greatly in later life stages due to the cessation of somatic and brain growth. This rate change reveals how using Alberch et al.'s (1979) model fails to account for changes in rate of development. A linear model is insufficient to assess heterochrony in true ontogenetic trajectories as it ignores the complexity of growth and development during ontogeny. New methods that take developmental shifts into consideration must be considered when studying ontogeny and heterochrony. Lieberman et al. (2007) attempt to correct for the non-linearity of ontogeny by examining the trajectories in distinct age groups, but this assumes that the biologically-determined rate of development can be defined by subjective categories of aging.

Finally, the results for the squama data set revealed no significant difference between species in morphology of the squama for PC1. Additionally, life stage was also not a predictor of squama shape change in the sample of infant and juvenile bonobos. These results indicate that there is not a significant difference in the shape of squama between species and between observed life stages for bonobos. It is speculated that this may suggest the squama does not change shape significantly throughout chimpanzee and bonobo ontogeny, though differences may arise during other developmental stages.

While the squama does not vary between species and life stages, the inclusion of the browridge causes the frontal to vary between both these variables. This indicates that the browridge is responsible for a large portion of the shape variation that occurs in the frontal during ontogeny. As a result, the author agrees with Bruner et al. (2013) and Athreya (2009) that the browridge should be studied separately from the frontal, and from the rest of the neurocranium as well, due to the amount of interaction it has with the face.

Several limitations must be considered alongside these results. Primarily, analysis of ontogenetic trajectory by life stage was hindered by the lack of adult and infant specimens for chimpanzees and adult specimens for bonobos. A larger, developmentally varied sample size would have allowed for a more complete assessment of heterochrony in the comparison between species. The results of the juvenile comparison could use additional evidence due to the fact that they represent an incomplete picture of the species' ontogenetic trajectories. While this is partially remedied by the analysis of the infant and juvenile bonobos, the analysis only shows a partial ontogenetic trajectory and the shifts in the rate of development for only bonobos.

Similarly, this study does not make use of more than the basic set of landmarks. The addition of pseudo- or semi-landmarks would have increased the strength of the results by allowing for a more complete analysis of the different shapes and contours of the frontal. For example, the browridge consists of four landmarks in this study; this is inadequate to completely measure the shape variation that occurred in the browridge during ontogeny. Additional landmarks would allow for the analysis of the supraorbital torus and post-orbital constriction among other frontal structures. Other methods of analyzing shape could also be employed to reveal the more subtle aspects of morphology

in the frontal. Athreya (2009) uses methods that create outlines of the curvature of the frontal. Methods such as these would be useful for more closely analyzing shape change during ontogeny.

Finally, knowledge of specimen sex in the sample was limited. This prohibited an analysis of the entire sample in regards to the differences between sexes in shape variation. While statistical tests on approximately half the sample did not detect any difference in shape variables between the sexes, a test of the full sample would have been statistically more powerful and informative. Unfortunately, this is a common problem with collections of this magnitude.

CHAPTER 7: CONCLUSION

In conclusion, this study used geometric morphometric methods to determine and compare shape change between chimpanzees and bonobo frontal bones. Specifically, differences in shape were assessed between juvenile chimpanzees and bonobos, and ontogenetic shape change was assessed in infant and juvenile bonobos. Results of ANCOVA models indicated that shape of the frontal was significantly different between the two species and the slope of the two regressions differed as well. These results hint at possibly divergent ontogenetic trajectories between species for the frontal bone in contrast to past research which found paedomorphism in the neurocranium. Analysis of the bonobo ontogenetic trajectory in infants and juveniles revealed a trend in ontogeny which is similar to what is expected for bonobo somatic growth. Specifically, infants appeared to have a lesser slope with juveniles having a greater slope, indicative of lesser and greater rates of development respectively.

In addition to the entire frontal, the same comparisons of shape change were made for the frontal without the browridge. Results indicated that the squama did not significantly differ in shape between chimpanzees and bonobos and did not significantly change shape between infant and juvenile life stages. When compared with the results of the frontal, these results indicated that a majority of the shape change in the frontal occurred in the browridge.

The purpose of this study was to analyze the differences in shape of the frontal between *Pan* species and to analyze the ontogenetic shape change for infant and juvenile bonobos. Overall these results raise questions about past methodology and results. Most importantly, this work shows that the inclusion of the browridge in studies of shape change in the neurocranium may lead to erroneous results due to the interaction between the browridge and the face. Based on the results found here, it is suggested that the browridge and squama, as part of the neurocranium, should be studied separately in order to avoid issues with said interaction. This suggestion is also found in other recent work as well (Athreya 2009; Bruner et al. 2013), confirming the importance of separating the two structures for studies of shape change.

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